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ORIGINAL ARTICLE

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Keywords Common marmosets · Pair bond · Telemetry · Sociophysiology · Confrontation · Ovarian cycle · Cardiophysiology · Behavior

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Introduction

Bonding has been a major term in early ethological studies and normally it refers to a motivational construct which keeps mother–infant dyads (mother–infant bond), pairmates (pair bond) or in general social partners (social bond) together (Bowlby 1974; Lorenz 1963). The quality and quantity of bonding, as well as its presumptive underlying mechanisms, are normally investigated through the behavioral responses of the observed individuals (Wickler 1976). The bond between socially monogamous pairmates is mostly assessed on the basis of proximity measurements and specific partner-restricted behaviors (Lamprecht 1973). Such behavioral syndroms permit definition of the bond between two pairmates in contrast to their relationship towards unfamiliar conspecifics (Mason and Mendoza 1998). In recent years very detailed work has been published on socio- and neuroendocrinology of pair-bonding in monogamous prairie voles (Carter 1998; Carter et al. 1995; Insel and Hulihan 1995; Insel and Shapiro 1992; Insel and Young 2001; Kirkpatrick et al. 1994). However, it is hard to imagine that comparable work will be achieved in the near future with a non-rodent mammal.

In primates, based on captive studies, many authors have assumed that marmosets and tamarins (Callitrichidae), are monogamous and that also free-ranging social groups are mostly family groups (Eisenberg 1977; Epple 1975, 1977; French and Snowdon 1981; Kleiman 1977; Leutenegger 1973, 1980; Poole 1978; Rothe 1975; Sutcliffe and Poole 1984). However, based on data from field studies the universal validity of the monogamous social structure for callitrichids has been questioned (Digby and Ferrari 1994; Sussman and Garber 1987). Nevertheless, in the wild as well as in captivity, for an established pair the presence of a strange conspecific constitutes for the opposite-sexed pairmate a social or even sexual alternative whereas for the same-sexed pairmate it constitutes a rival, i.e. a threat to the integrity of the pair bond (Anzenberger 1993).

From several previous studies, it is known that common marmosets often behave aggressively towards opposite-sexed strangers when their own mate is present (Anzenberger 1985, 1993; Evans 1983; Sutcliffe 1980; Sutcliffe and Poole 1984). Furthermore, common marmosets show a high level of intrasexual aggression (Evans 1983). The observations of intrasexual aggression, combined with the finding that paired animals show more aggressive behaviors towards opposite-sexed stranger when the familiar pairmate is present, suggest that common marmosets are considerably more aggressive in the presence of the familiar pairmate than they are individually (Evans 1983). However, in the absence of the pairmate, common marmoset females are indifferent to novel males, whereas males actively solicit contact and even sexual interactions with novel females (Anzenberger 1985; Evans 1983).

Several experimental studies investigating the pair bond have yielded a sound body of knowledge about bonding and social dynamics in different primate species [titi monkey, *Callicebus moloch* (Anzenberger 1988; Anzenberger et al. 1986; Cubicciotti and Mason 1975, 1978; Fernandez-Duque et al. 1997; Mason 1975; Mendoza and Mason 1986); common marmoset, *Callithrix jacchus* (Anzenberger 1985, 1993; Epple 1970; Evans 1983; Evans and Poole 1983; Harrison and Tardif 1989); black tufted-ear marmoset, *C. kuhli* (Smith et al. 1998); cottontop tamarin, *Saguinus oedipus* (French and Snowdon 1981; Harrison and Tardif 1989); saddleback tamarin, *S. fuscicollis* (Epple 1990); red-bellied tamarin, *S. labiatus* (Buchanan-Smith and Jordan 1992); golden lion tamarin, *Leontopithecus rosalia* (French and Inglett 1989; Inglett et al. 1990)]. However, almost nothing is known about the physiological correlates of the pair bond. In primatology, a few investigations have focused on cardiophysiological correlates of mother–infant relationships (Reite et al. 1974) or of social partners (Boccia et al. 1989; Preston et al. 1996), albeit only with very small sample sizes. Behavioral tests with parallel recording of cardiophysiological data on pairmates have first been made on the titi monkey (Cubicciotti and Mason 1975). In that study, heart rate was recorded with a non-invasive telemetry system, providing the opportunity to obtain quantitative access to one physiological correlate of the pair bond, coined "emotional attachment." There was a follow-up study on the cardiophysiology of the pair bond of *C. moloch* (Cubicciotti and Mason 1978) but there is a complete lack of comparative data on other socially monogamous primate species. Therefore, the aim of the present study was to investigate behavioral and, in parallel, cardiophysiological responses of mated individuals of common marmosets to confrontations with an opposite-sexed conspecific: First, in the presence of the familiar pairmate and second, in the absence of the familiar pairmate. This two-fold experimental approach allows one to separate the individual contributions of the two pairmates to the pair-bond.

Methods

Animals

Test-individuals were six established pairs of healthy and normotensive common marmosets (*C. jacchus*) aged 3–7 years, housed at Novartis Pharma AG (Basel, Switzerland). Pairmates have been together at least 18 months prior to this study. Body weights (mean ± SD) for males were 387.2 ± 17.5 g and for females 431.5 ± 37.5 g. For confrontations, members of another seven established pairs were used. All males of the colony were vasectomised in order to exclude breeding, therefore, all test males and test females did never reared offspring with the actual or a prior pairmate. Every pair was housed in a stainless steel cage of 1.60×1.20×0.9 m. Test and confrontation animals were kept under identical conditions but in different rooms which were ventilated with air maintained at a temperature of 24–27°C and a humidity of 50–80%. Light was on from 6:00 a.m. to 6:00 p.m. The animal rooms were not sound-isolated and therefore, auditory contact was possible. The animals were fed a normal-salt pellet diet containing Na^+ (100-mmol/kg) and K^+ (250-mmol/kg) (NAFAG, Gossau, Switzerland), supplemented with fruits, eggs, meat and milk. Water was available ad libitum.

Experimental design and procedure

The six test-males and six test-females were used in three replicates each, yielding a total of 36 trials. A trial was divided into four consecutive segments during which cardiophysiological and behavioral measurements were taken: baseline (10 min); confrontation while the pairmate was present (10 min); confrontation while the pairmate was absent (5 min); reunion (10 min). The experimental design, when the test-individual was the male, is shown in Fig. 1. During baseline, the test-individual was left undisturbed with its pairmate in the home cage. During confrontation, the test-individual as well as an opposite-sexed stranger were transferred to an unfamiliar cage (confrontation cage) in an unfamiliar room. However, design and dimensions both of cage and room were identical to the situation in the home area of the test animals. The test-individual's pairmate was also transferred to the unfamiliar room to occupy another cage (pairmate's cage) 1 m opposite the confrontation cage. Thus, the test-individual's pairmate was physically present during the confrontation of the individual with an opposite-sexed stranger. After measuring the responses during confrontation while the pairmate was present, the confrontees were separated by a wire screen but remained in the confrontation cage, while the pairmate was returned to the home cage. Subsequently the confrontees were again allowed together for a further period of 5 min and the confrontation started in the absence of the pairmate. This was done to investigate a possible controlling effect of the pairmate's presence on

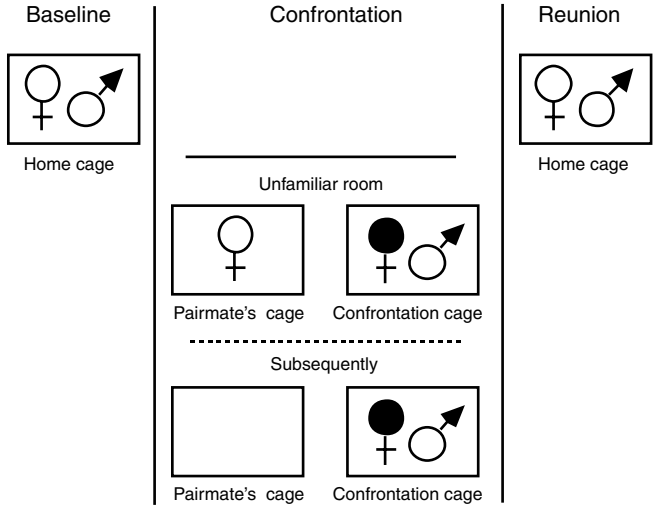

Fig. 1 Experimental design of a trial when the test-male was confronted with a strange female. Male (*open symbol*) = test-individual, female (*open symbol*) = pairmate, female (*black symbol*) = strange female

the interactions between the confrontees. If the pairmate had no effect, the confrontees should show the same responses regardless of its presence or absence. When both conditions are imposed immediately one after the other, any behaviors withheld by the confrontees (during the pairmate's presence) should become visible (during the pairmate's absence). In an earlier study (Gerber et al. 2002), the first mounting between unfamiliar animals occurred within two and a half minutes and this finding determined the 5-min test duration applied here. During reunion, data were collected when the test-individual had been returned to its pairmate in the home cage.

For transportation of the animals from the home cage to the confrontation cage and back, the animals have been trained to enter on demand transportation boxes which were attached to the cage front.

Testing was done on 3 days per week with 1 or 2 days in between. Two trials were conducted per day, one in the morning, the other in the afternoon, allowing the testing of six different animals per week. Morning and afternoon trials were balanced across individuals and males and females completed the first, the second and finally the third trials on alternating weeks. There elapsed at least 4 days between consecutive trials of the same test-individual. Every test-individual was confronted with the same stranger only once to exclude familiarity between the animals. The study was performed under the license No. 1329 for animal experimentation issued by the Federal Veterinary Office (Veterinäramt Basel Stadt) and in full accordance with the governmental guidelines of Switzerland.

Recording of behavior

For recording of behaviors, a miniaturized remote-controlled video camera (65×8×55 mm; Video and Optical Systems Ltd., England) was installed within the cages. After all experiments had been completed, the videotapes have been analyzed by recording various behavioral elements with the aid of a datapad recorder (Zirelco Datapad ZE661). Behaviors were classified in four different categories: aggressive behaviors (vocal threat, cuffing, attacking, fighting), courtship behaviors [nuzzling, lip-smacking (males), lip-smacking with tongue-flick (females)], sexual behaviors (genital inspection, mounting, thrusting, penis-licking) and affiliative behaviors (sitting in body contact, grooming invitation, grooming). The behavioral elements used, followed the descriptions of several authors (see Gerber et al. 2002). Phee calls were also recorded which are used both in intra- as well as intergroup communication and have sex-specific characteristics (Norcross et al. 1999). For all elements actual frequencies were recorded and in addition, duration measures were used for sitting in body contact, grooming and mounting.

During a trial only one member of the pair (=test-individual) served as focal animal, i.e. for that individual behaviors and cardiophysiology (see below) were recorded in parallel. From the partners only those behavioral elements were recorded when they were directed towards the test-individual, e.g. when during baseline or reunion the pairmate, or during confrontation the stranger, initiated aggressive, affiliative, courtship or sexual behaviors towards the test animal.

Telemetry system

Cardiophysiological data and locomotor activity have been recorded with a telemetry and data acquisition system from Data Sciences (St. Paul, MN, USA). This system allows the continuous recording of blood pressure, heart rate and locomotor activity in freely moving marmosets. The transmitters were implanted under aseptic conditions and anesthesia into the peritoneal cavity of each test-individual by one of the authors (C.R. Schnell). Figure 2 shows a *C. jacchus* of our colony wearing an implanted transmitter. Anesthesia was induced by using intramuscular alfaxalonum (10 mg/kg; Saffan, Glaxovet, Uxbridge, UK), atropine (0.15 mg/kg; Atropin, Sigfried, Zofingen, Switzerland), and diazepam (0.75 mg/kg; Valium, Roche, Basel, Switzerland). The animals received, immediately after surgery, penicillin (5,000 IU; Duplocilline LA, Veterinaria, Zürich, Switzerland) and piroxicam (2 mg; Piroxicam-Mepha, Mepha Pharma, Aesch/BL, Switzerland) intramuscular. Further information on the implantation technique are described elsewhere (Schnell and Wood 1993). The implantation of the transmitters was performed under an experimental license (no. 95) issued in accordance with the Veterinäramt Basel Stadt, Switzerland.

The computer was configured to record data, measured for 11 s with a sampling rate of 250 Hz, in cyclic runs of 1 min. Mean values of systolic and diastolic blood pressure (mmHg), heart rate (beats per min; bpm)

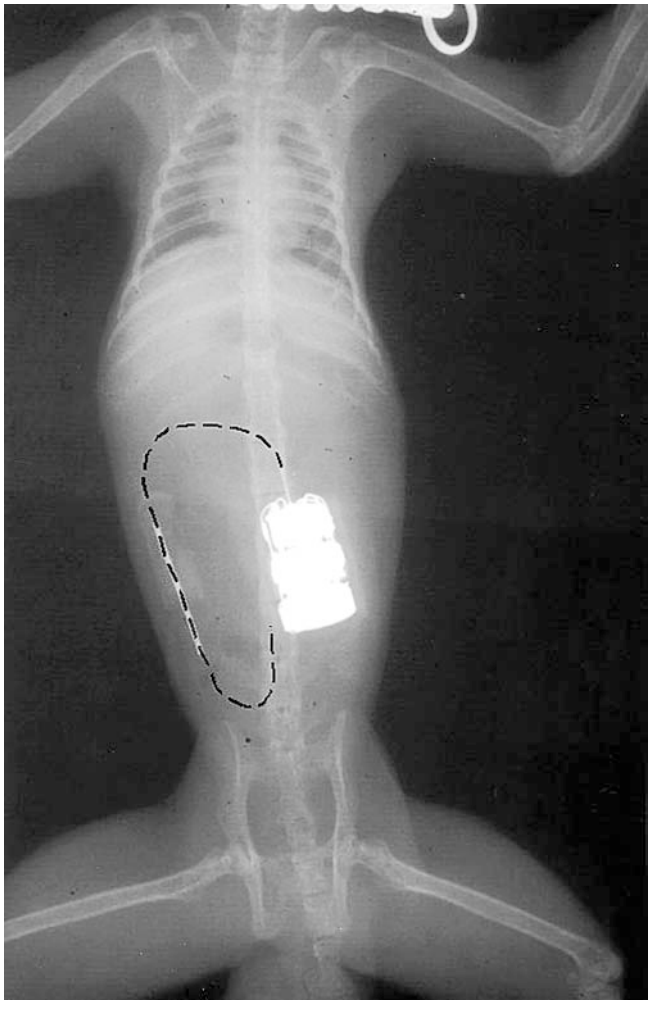

Fig. 2 X-ray image of a *C. jachus* wearing an implanted transmitter

and locomotor activity (movements per 2 min; mp2m) were then computed and stored. Locomotor activity was measured using the variability in the received signal strength as a result of changes in the distance and orientation relative to the receiving antennae. When both pairmates were in the same cage, data was only recorded from the test-individual because all transmitters used the same frequency. From the strange conspecific cardiophysiological data were not collected. For further information see Gerber et al. (2002).

Hormone analyses

To monitor the ovarian cycles of the test-females urine samples, collected five times a week during the whole duration of the study, were analyzed for their estradiol-17β (E_2) concentrations. Urine collection and hormone analyses are fully described elsewhere (Gerber et al. 2002). The day of ovulation was visually inferred from the hormone profiles of the female individuals as described by Hodges and Eastman (1984). In a few words, 4–5 days before ovulation estradiol-17β-levels sharply fall and remain low for a period of about 8 days during which ovulation occurs. After these days the E_2/Cr (E_2/Creatinine) levels increase markedly and remain elevated for about 17 days until the next sharp decline occurs indicating the next ovulation. The approximate day of ovulation can therefore be estimated by calculating 4 days back from the substantial increase after the days of low E_2/Cr levels. In the present paper, the estimated day of ovulation ± 2 days is referred to as "mid-cycle" (see also Fig. 1 in Gerber et al. 2002).

Determinations of ovarian cycles of the female individuals were only done after finishing all behavioral experiments. This means that during the trials no information was available on whether the females were in estrus or not.

Statistical analysis

In the present study, nonparametric tests have been used throughout. Significance level was set at $p \leq 0.05$, two-tailed. Differences across the alternative segments were tested using the Friedman two-way analysis of variance by ranks (subsequently named Friedman test). To determine which differences among segments were significant, multiple comparison was used post hoc (Siegel and Castellan 1988, p 180).

Results

Behavioral responses of male individuals during confrontations

The total frequencies of the behavioral elements which occurred during the two confrontation conditions are shown in Table 1. Male individuals did not show phee calls during confrontation with the strange female in the presence of their familiar female (PP) but during confrontation while the familiar female was absent (PA). Vocal threats were observed by male individuals and strange females during PP, but not during PA. Courtship behaviors were only performed by male individuals and only during PP. Mounts occurred in both confrontation conditions. Once, mounting did not occur during PP but subsequently during PA.

Behavioral responses of male individuals during baseline and reunion

Male individuals did not show phee calls when together with their mates in the home cage. Aggressive behaviors were not observed between established pairs, courtship behaviors (lip-smacking) were only performed by male individuals, sexual behaviors were absent and affiliative behaviors were shown. During baseline, females initiated sitting in body contact less often than males did [males: 24 times in eight trials ($N = 5$), females: nine times in five

trials ($N = 4$)]. However, when females initiated sitting in body contact, the median duration lasted 7 times longer than when this behavior was initiated by males (males: 10 s/females: 70 s). During reunion, females initiated sitting in body contact less often than males did [males: 27 times in nine trials ($N = 5$), females: 13 times in eight trials ($N = 4$)] and again the median duration was longer than when males initiated this behavior (males: 9 s, females: 51 s). During baseline, males groomed their females nine times in four trials ($N = 4$) and during reunion ten times in six trials ($N = 3$). Females however, never groomed their males. About one third of male grooming was initiated by a grooming invitation made by the females.

Cardiophysiological responses of male individuals

During both confrontation conditions (PP and PA) all cardiophysiological parameters were significantly higher compared to baseline ($p \leq 0.05$; Fig. 3). During reunion males showed almost baseline values or at least lower values than during confrontation and diastolic blood pressure (DBP) was significantly lower during reunion compared to the confrontation conditions. Locomotor activity did not differ across the different segments and as such was not responsible for the differences in cardiac activity.

Behavioral responses of female individuals during confrontations

The total frequencies of the behavioral elements which occurred during the two confrontation conditions are shown in Table 2. Female individuals showed phee calls during both conditions. They called almost twice as often during PP as during PA. As in male individuals, vocal threats were only observed during PP, i.e. while the familiar male of the female individual was present. In addition, two female individuals even attacked the strange males. Courtship behaviors were shown by both sexes: During PP, the strange males showed nuzzling and, female individuals showed lip-smacking during both confrontation segments. Mounts, almost half of them including thrusting, occurred in both confrontation conditions involving two female individuals.

Behavioral responses of female individuals during baseline and reunion

Female individuals did not emit phee calls when they were together with their familiar males in the home cage. Aggressive behaviors were not observed. Courtship behaviors occurred during reunion: Female individuals showed lip-smacking and their mates showed nuzzling. Sexual behaviors were absent. Affiliative behaviors occurred. During baseline, males initiated sitting in body contact less often than females did [males: eight times in five trials ($N = 3$), females: 13 times in seven trials ($N = 5$)]. During reunion, males initiated sitting in body contact more often than females did (males: 24 times in 12 trials ($N = 6$), females: four times in four trials ($N = 4$)). However, median duration was about three times shorter than when females initiated this behavior (males: 6 s, females: 16 s). During baseline, males groomed their females about twice as often as females [males: nine times in four trials ($N = 3$), females five times in two trials ($N = 2$)]. During reunion, males groomed their females seven times in four trials ($N = 3$), two times after the females made grooming invitation. Females never groomed their males during reunion.

Cardiophysiological responses of female individuals

A comparison of the cardiophysiological values across the different segments (Fig. 4) revealed no significant differences except for heart rate which was significantly higher during PP and PA compared to baseline. Locomotor activity did not differ across the different segments.

Female cycles and mounting events

The average cycle length of five of the total six females was 32.8 ± 7 days (mean $\pm$ SD; total cycles: 11). In one

Table 1 Behavioral responses during confrontations of male individuals

While	Pairmate present (PP) behavioral elements shown by		Pairmate absent (PA) behavioral elements shown by	
	Male individuals	Strange females	Male individuals	Strange females
Phee call	0	–	21(5) $N = 3$	–
Vocal threat	3(2) $N = 2$	4(3) $N = 3$	0	0
Lip-smacking	2(2) $N = 2$	0	0	0
Nuzzling	7(4) $N = 3$	0	0	0
Mounting	3(3) $N = 3$	–	2(2) $N = 2$	–

Total frequencies of the observed behavioral elements during confrontations of male individuals with a strange female. The numbers indicate the total frequency of the behavior. In parentheses is the number of trials in which the behavioral elements occurred (total 18 trials per experiment)

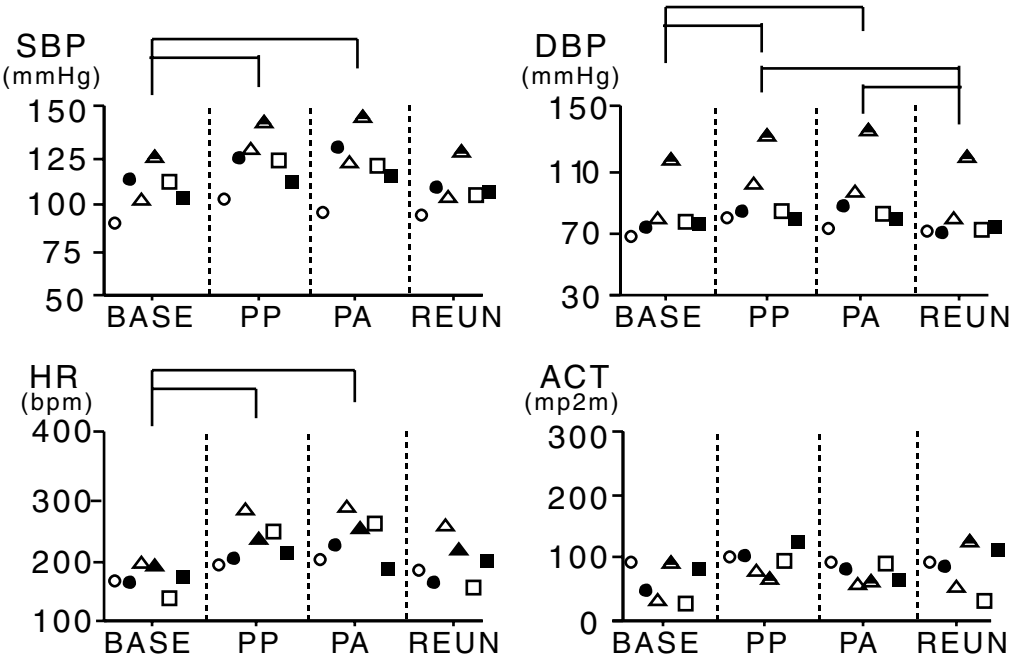

Fig. 3 Cardiophysiological results and locomotor activity for male individuals during baseline (*BASE*), confrontation in the presence of the pairmate (*PP*), confrontation in the absence of the pairmate (*PA*) and during reunion (*REUN*). The values are given for each individual by different symbols. *SBP* systolic blood pressure, *DBP* diastolic blood pressure, *HR* heartbeat rate, *ACT* locomotor activity. (*mmHg* millimeters of mercury, *bpm* beats per min, *mp2m* movements per 2 min). *Solid lines* indicate significant differences ($p \leq 0.05$) between two conditions

female, no cyclic changes could be determined. However, on the behavioral level this female responded in the same way as the other animals. From the strange females no urine samples were collected, i.e. no ovarian cycles could be determined.

The hormone analysis which were done after finishing all behavioral experiments revealed that all (with the exception of two) trials were conducted when the females were in the non-fertile phase of the ovarian cycle. In one of these two trials conducted within the fertile phase, mounting occurred during both confrontation conditions. All other mounts occurred out of the mid-cycle phase of the females.

Discussion

In the study presented we investigated the responses of mated common marmosets to confrontations with an opposite-sexed stranger while their own pairmate was present or absent. Any behavioral differences between these two conditions are suitable to illustrate two aspects of the pairbond. First, the individual's contribution to it and second, the pairmate's controlling effect on it.

Common marmosets are known to be rather aggressive towards opposite-sexed conspecifics when their pairmates are present (Anzenberger 1985; Evans 1983; Gerber 1999; Gerber et al. 2002; Sutcliffe 1980; Sutcliffe and Poole 1984). In addition, it has been shown for other callitrichids that males respond with more aggression towards a male intruder and females respond with more aggression towards a female intruder (French and Inglett 1989; French and Snowdon 1981; French et al. 1995; Schaffner et al. 1997). Such intra-sexual aggression can ensure mating exclusivity by preventing individuals of the same sex contacting the mate and provides an important contribution to the stability of the pair bond [Epple (1977) for saddleback tamarins, Tenaza (1975) for Kloss' gibbon, *Hylobates klossii*]. In a confrontation study on common marmosets (Anzen-

Table 2 Behavioral responses during confrontations of female individuals

While	Pairmate present (PP) behavioral elements shown by		Pairmate absent (PA) behavioral elements shown by	
	Female individuals	Strange males	Female individuals	Strange males
Phee call	56 (8) $N=4$	–	32 (7) $N=3$	–
Vocal threat	21 (5) $N=3$	9 (5) $N=4$	0	0
Attack	8 (3) $N=2$	0	0	0
Lip-smacking	5 (3) $N=3$	0	4 (3) $N=2$	0
Nuzzling	0	8 (5) $N=3$	0	0
Mounting	–	4 (2) $N=2$	–	4 (2) $N=2$

Total frequencies of the observed behavioral elements during confrontations of female individuals with a strange male. The numbers indicate the total frequency of the behavior. In parentheses is the number of trials in which the behavioral elements occurred (total 18 trials per experiment)

berger 1985), female cuffing, biting and attacking occurred quite often, whereas in the present study female attacks could be recorded only occasionally. In general, female individuals did act more aggressively towards strange males than vice versa but neither sex responded highly aggressively towards opposite-sexed strangers. The low intensity of aggressive behaviors shown by the mated individuals of the present study might be attributable to the strength of the pair bond. The females here, although mated with the actual male for at least 18 months prior to this study, never became pregnant because all males were vasectomised. Probably, the pair bond was not as strong as in pairs that produced offspring (as it was the case in the study by Anzenberger 1985), because rearing offspring together possibly consolidates the pair relationship. Accordingly aversive behaviors towards strange conspecifics, in order to conserve the pair's socio-sexual integrity might have been diminished. We might speculate that when pairmates of common marmosets have limited reproductive success with the existing partner, then they would show more interest and therefore, less aggressive behavior towards unfamiliar opposite-sexed conspecifics than when they are successful breeders. A further reference to the hypothesis that the pair bond was weakened in the pairs used for the present study was the occurrence of courtship behaviors and sexual behaviors (including mounting), despite the presence of the familiar pairmate. In former studies (Anzenberger 1985; Evans 1983), this was only the case when the familiar pairmate was absent.

For male individuals, after having seen their mates interacting sexually with a strange male, it could be expected that they would mount their females upon reunion in the home cage. On the one hand such behavior might function for sperm competition reasons and on the other hand to reaffirm the pair bond. However, mounts were never observed during reunion. Common marmosets are able to recognize the different phases of the ovarian cycle of conspecifics from olfactory cues (Smith and Abbott 1998). In the present study only two trials fell into the mid-cycle phase of two female individuals. Therefore, we assume that in trials when the female individuals were not in the mid-cycle phase there was no need for the familiar male to mount the female for sperm competition effects during reunion although the female was mounted by the strange male during confrontation. It would be interesting to investigate whether or not males mount their females more often during reunion when the females are in the mid-cycle phase and have been mounted during a preceding confrontation.

Sitting in body contact and grooming can be regarded as expressions of bonding motivation. These behaviors should be particularly prominent when the pairmates are reunited after confrontation. Male individuals initiated sitting in body contact clearly more often than females. We therefore conclude that the male is the prime initiator in maintaining pair proximity, which is corroborated by earlier findings (Poole 1978). In addition, male and female pairmates showed higher frequencies of initiating sitting in body contact during reunion compared to baseline, which might have been indicative of reaffirmations of the pair bond.

We observed that after aggressive behaviors have occurred during confrontations while the pairmate was present the animals mainly tried to avoid each other also in the absence of the pairmate. This probably led to

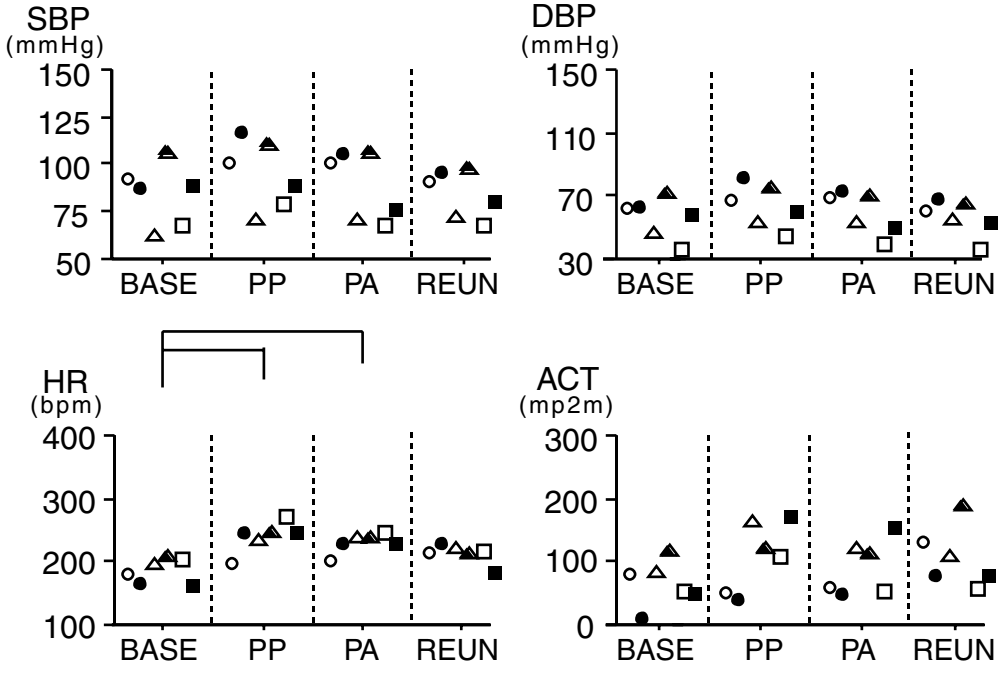

Fig. 4 Cardiophysiological results and locomotor activity for female individuals. Abbreviations see Fig. 3. Same symbols as in Fig. 3 represent values of actual pairmates

lower frequencies of aggressive behaviors and no further attempts of sexual behaviors during confrontation in the absence of the pairmate.

Concerning cardiophysiology, confrontation with an opposite-sexed stranger clearly affects common marmosets regardless of the presence or absence of the familiar pairmate. The physiological arousal during confrontation could derive from being in an unfamiliar environment separated from the pairmate. These responses have been investigated in an earlier paper (Gerber et al. 2002). We showed there that separation does increase cardiovascular activity and that these adverse effects are buffered by the familiar environment, i.e. were less pronounced when separated animals remained in the home cage. On the other hand, while in the unfamiliar environment together with a companion, heart rate values were lowered when the companion was the pairmate but not when it was an opposite-sexed stranger. It follows that the arousal comes from two sources, the unfamiliar environment as well as the social quality of the companion. In the present study the confrontations were conducted in an unfamiliar environment in order to place both confrontees in identical situations. If the confrontations had been conducted in the home cage, the pairmate although physically removed, would still be olfactorilly present which might influence the behavior of the confrontees. Furthermore, common marmosets are known to be territorial, i.e. they defend their home range against conspecific intruders (Hubrecht 1985). Therefore, when investigating responses towards opposite-sexed stranger, the best approach is to conduct the confrontation in a ''neutral'' zone to avoid environmental bias. Otherwise, the occuring or lacking behaviors, respectively, may be attributable to the environment rather than to the confrontation situation.

In the study presented here, we focused on the responses of common marmosets to confrontations with an opposite-sexed stranger while the former's pairmate was present or absent. This comparison has been done to investigate a possible controlling effect of the pairmate's presence on interactions between the confrontees. When both conditions are conducted immediately one after the other, any behaviors withheld by the confrontees during the pairmate's presence, should become visible during the pairmate's absence. If during the confrontation on the pairmate's presence sexual behaviors do not occur but subsequently when the pairmate is removed, the missing sexual behaviors must be attributable to the suppression by the pairmate's presence.

All cardiophysiological parameters of male individuals were significantly higher during both confrontation types compared to baseline. Female individuals also showed increased cardiophysiological values during these confrontations but only heart rate was significantly higher compared with baseline. These increases were not simply attributable to increased locomotor activity. In fact, during reunion, male and female individuals showed higher locomotor activity than during the preceding confrontation segment (while the pairmate was absent) whereas the cardiophysiological values were in general lower. Taking increased heart rate as an indicator of arousal, confrontation while the pairmate is absent thus appears to be more arousing than when the pairmate is present. A possible explanation for this finding could be social support, provided by the presence of the familiar pairmate during confrontation. This effect has been shown for several species [e.g., titi monkey (Cubicciotti and Mason 1975; Mendoza and Mason 1986); black tufted-ear marmoset (Smith et al. 1998); guinea pig (Sachser 1992)]. Evans (1983) introduced established pairs of common marmosets to single unfamiliar conspecifics and found that paired males tended to direct more aggression towards unfamiliar males than females did, and that paired females were more aggressive to unfamiliar females than males. Higher levels of intra- as opposed to inter-sexual aggression have also been reported for the saddleback tamarin (Epple 1977), the cottontop tamarin (French and Snowdon 1981) and the golden lion tamarin (Inglett et al. 1990). Accordingly, the main actor in expelling a stranger should be the same-sexed pairmate, and its presence may cause a reduction in arousal for the individual during confrontation.

Any definition of monogamy has to distinguish between two main concepts, the social system and the mating system (Anzenberger 1992; Wickler and Seibt 1983). Monogamy as a mating system means exclusivity of copulation, whereas monogamy as a social system means that a bond exists between the pairmates, i.e. some other social behaviors are exclusively performed between pairmates. In the present study, affiliative behaviors were never observed between unfamiliar animals. Sitting in body contact as well as grooming are behaviors that are regarded as consolidating the pair bond. Therefore, these behaviors are expected to occur only within established pairs, which is in accordance with our findings. In summary, the findings of the present study confirm the existence of a monogamous social system in common marmosets, whereas a monogamous mating system was not found in complete form.

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